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Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in response to light acclimation

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Abstract: Background: Acclimation to light is a driver of tropical forest dynamics and key to understanding the coexistence of dipterocarps, and how their demographic rates and traits trade-off. Aims: We examined light niche divergence in six dipterocarp species and hypothesised that seedlings can be functionally grouped, and allocate resources to either growth or storage in response to light changes. Methods: A pot experiment was performed to measure size-specific growth rate, wood density and total non-structural carbohydrate (NSC) concentrations of dipterocarp seedlings exposed to a simulated gap opening. Results: Light-demanding species responded to a gap opening with increased growth and decreased wood density, whereas shade-tolerant species showed a greater relative increase in NSC concentration. Iditol – an alditol – was identified, and *Dryobalanops lanceolata* responded to a gap opening with a significantly smaller increase in alditol concentration compared to other species. Conclusions: We group light-demanding and shade-tolerant species based on their acclimation to light and show that a generalist species is unique based on its response of NSC concentration to a gap opening. Our findings emphasise that the ecology of these species needs to be further studied in the context of their physiology to support their effective use in large-scale forest restoration efforts.

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1 **Title**

2 Growth rates and relative change in non-structural carbohydrates of dipterocarp seedlings in
3 response to light acclimation

4
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10

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12 The authors declare that they have no conflicts of interest. The authors acknowledge that they have
13 no financial interest or benefit arising from the direct applications of this research.
14

15 **Notes on Contributors**

16 **Philippe Saner** is an environmental scientist with a main interest in tropical plant community
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1 **Lindsay A. Turnbull** is an associate professor with a research interest in how and why plant
2 species are so different to each other, and what the consequences of these differences may be for
3 ecosystems.

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5 stability and functioning of ecosystems and the provision of ecological services.

6

7 **Figures:** 5

8 **Tables:** 1

9 **Electronic supplementary material:** 1 figure

1 **Abstract**

2 **Background:** Acclimation to light is a driver of tropical forest dynamics and key to understanding
3 the coexistence of dipterocarps, and how their demographic rates and traits trade-off.

4 **Aims:** We examined light niche divergence in six dipterocarp species and hypothesised that
5 seedlings can be functionally grouped, and allocate resources to either growth or storage in response
6 to light changes.

7 **Methods:** A pot experiment was performed to measure size-specific growth rate, wood density and
8 total non-structural carbohydrate (NSC) concentrations of dipterocarp seedlings exposed to a
9 simulated gap opening.

10 **Results:** Light demanding species responded to a gap opening with increased growth and decreased
11 wood density, whereas shade-tolerant species showed a greater relative increase in NSC
12 concentration. Iditol—an alditol—was identified, and *Dryobalanops lanceolata* responded to a gap
13 opening with a significantly smaller increase in alditol concentration compared to other species.

14 **Conclusions:** We group light demanding and shade-tolerant species based on their acclimation to
15 light and show that a generalist species is unique based on its response of NSC concentration to a
16 gap opening. Our findings emphasize that the ecology of these species needs to be further studied in
17 the context of their physiology to support their effective use in large-scale forest restoration efforts.

18

19 **Keywords**

20 Borneo, dipterocarps, NSC concentration, iditol, demographic rates, functional traits, size-specific
21 growth rate, light acclimation, shade-tolerants, light demanders

22

1 **Introduction**

2 The ecology of tropical tree species has been studied extensively at the seedling stage and in
3 response to light, a main driver of tropical forest dynamics (Augsburger 1984; Bloor 2003; Baltzer
4 & Thomas 2007; Baraloto & Forget 2007; Philipson et al. 2012; Paine et al. 2015). Some studies
5 have tested how seedlings respond to changes in light availability that occur during sudden gap
6 formation or closure caused by tree- or branchfalls in a natural forest (Osunkoya and Ash 1991;
7 Parsons et al. 1994; Huante and Rincon 1998; Dalling et al. 2004; Philipson et al. 2014). Such
8 events dramatically alter both light availability and microclimatic conditions and offer a potential
9 regeneration niche axis along which species may be differentiated (Canham 1989; Denslow et al.
10 1998; Poorter 2005; Marthews et al. 2008). Early theoretical concepts on the importance of canopy
11 gap dynamic processes and how they drive the coexistence of tree species, such as the gap size-
12 niche partitioning (Connell 1978; Hartshorn 1978; Denslow 1980) or cross-over point irradiance
13 (Givnish 1988; Latham 1992; Sack and Grubb 2001), have been challenged for their over-simplicity
14 (Brokaw and Scheiner 1989; Raich and Christensen 1989; Brown and Whitmore 1992; Barker et al.
15 1997; Agyeman et al. 1999; Brown et al. 1999; Kitajima and Bolker 2003; Baraloto et al. 2005).
16 Mean growth rate may be positively correlated between low-light and high-light conditions and thus
17 show no rank reversal in performance among species, however comparison of mean growth rate and
18 survival for the same species may still reveal a trade-off.

19 These initial ideas of driving mechanisms that promote species diversity have been further
20 explored by expanding the spatial and temporal limits. One example is the observed trade-off in
21 seedlings to grow rapidly under high-light environments of large canopy gaps, versus the ability to
22 survive in low-light conditions typical of the forest understory (Hubbell and Foster 1992; Kitajima
23 1994; Kobe et al. 1995; Poorter 1999). In addition, the idea of ontogenetic niche shifts and the
24 divergence in regeneration niches were framed to explain how acclimation to light (light niche
25 divergence) may promote coexistence by allowing species to partition forest light conditions
26 (Myers and Kitajima 2007; Poorter and Kitajima 2007; Kitajima and Poorter 2008). For example,

sudden increases or decreases in light may force a seedling to selectively allocate resources into structural tissue for current growth (e.g. diameter) to outcompete others for access to light or, invest into denser wood or non-structural carbohydrate (NSC) storage to prolong survival (Kobe 1997; Canham et al. 1999; Poorter et al. 2010). Although similar questions on light niche divergence have been tackled before, this study contributes to the comparative body of literature by adding results from a pot experiment with dipterocarp seedlings where we experimentally simulated a gap opening event to study the effect on seedling ecophysiology with seedlings that are widely used in large-scale forest restoration efforts (Hector et al. 2011).

The members of the *Dipterocarpaceae* (dipterocarps) family (Wyatt-Smith 1995) contribute about 50% of the upper canopy trees in undisturbed lowland mixed dipterocarp forests and comprise the majority of commercial timber extracted from South East Asia (Symington 1943; Ashton 1982). Dipterocarps offer an ideal study system to test these proposed trade-offs between investing into growth or storage. They belong to the shade-tolerant climax species, but within this general category have species-specific differences based on their wood density and acclimation to light (Gustafsson et al. 2016). Philipson et al. (2012) assessed trade-offs in growth rates of dipterocarp seedlings and observed substantial crossovers among 21 species and no consistent growth hierarchy across light treatments. This may indicate that the heterogeneity of the light environment is a driving force to promote diversity in dipterocarps. Further, they assessed trade-offs between mean growth rate and survival with a cross-comparison among 15 species—covering five out of the six species in the present study—where the relationship in basal diameter growth and probability of mortality was found to be positive (Philipson et al. 2014). In addition, this recent study reported a negative relationship between wood density and the probability of mortality, suggesting that wood density can serve as a surrogate for survival in the dipterocarp seedlings of this study.

Apart from the trade-off in structural tissue (growth and wood density) an additional key trait that received attention lately is NSC. Recent findings on eight dipterocarp seedlings—including

1 four of the species of this study—show that NSC can be linked to increased survival under simulated
2 drought conditions (O’Brien et al. 2014, 2015). Further, soluble sugar concentration, but not starch
3 concentration, was reported to significantly increase in woody tissue and decrease in leaf tissue of
4 *Shorea beccariana* and *S. parvifolia* seedlings in response to a simulated drought over 20 days
5 (Valtat 2015). This shows that carbohydrates may fulfill diverse roles during plant metabolic
6 adaptation to increased stress and mortality (McDowell and Sevanto, 2010). To what level NSC are
7 involved in whole plant acclimation to light is currently unknown for dipterocarps and so is the role
8 of water-soluble carbohydrates (WSC), and specifically alditols. Proposed ecophysiological
9 functions of alditols in plants are manifold and include primary products of photosynthetic carbon
10 assimilation, translocation and storage of carbon, and abiotic stress protection (e.g. as compatible
11 solutes, osmoregulators, and antioxidants) (Bielecki, 1982; Loescher & Everard, 2000). As primary
12 photosynthetic products, alditols may be stored in source leaves and/or exported to sink tissues
13 where they may also be stored and/or used for growth. Their storage function is illustrated by the
14 fact that alditols may easily accumulate to 10-20% of a tissue’s dry weight (Dietz & Keller, 1997;
15 Loescher & Everard, 2000).

16 Hence, the motivation of this study is to elaborate on these latest findings on trade-offs
17 within, and between, key functional traits in dipterocarps, by forcing seedlings into an altered
18 carbon balance in a pot experiment to study light niche divergence. We experimentally test for
19 species-specific light acclimation strategies in the relative change of carbohydrates to structural
20 tissue to support growth or wood density versus the proportional change in total NSC concentration
21 or alditol concentration. Our initial hypothesis is that relative changes in selected life history
22 attributes in response to light acclimation allow for grouping dipterocarps into light demanders and
23 shade-tolerants, including a generalist species. Based on previous findings in the literature, we
24 predict that shade-tolerants and the generalist species will show a relative change in carbohydrates
25 towards denser wood—a trait that positively correlates with survival—whereas light demanders will
26 increase their mean relative growth. Further, we expect that shade-tolerant species and the

1 generalist, as a direct response to light acclimation, will show a greater proportional change in
2 carbohydrate concentration, whereas light demanding species will increase their mean relative
3 growth.

5 **Materials and methods**

6 *Experimental set-up*

7 The study site (05°05'20'' N, 117°38'32'' E, 102 m.a.s.l.) was located in the Malua Forest Reserve
8 in the eastern part of Sabah in Malaysian northern Borneo. Six climax dipterocarp species native to
9 Sabah and widely used for forest rehabilitation (Sabah Forestry Department 2008) were selected for
10 this pot experiment based on their known range in wood density (Newman et al. 1998) and differing
11 response in light acclimation (Moad 1992; Zipperlen 1997; Clearwater et al. 1999): *Dryobalanops*
12 *lanceolata*, *Hopea nervosa*, *Shorea argentifolia*, *Shorea leprosula*, *Shorea macroptera* and *Shorea*
13 *parvifolia*. Four of them are classified as endangered (*D. lanceolata*, *S. argentifolia* and *S.*
14 *leprosula*) or critically endangered (*H. nervosa*) according to the IUCN Red List (2015) and it is
15 therefore essential to better understand their ecology.

17 *Study design*

18 The experimental design consisted of ten shade houses (4 x 6 x 5 m) that were aligned in five
19 blocks of two, randomly allocated to high or low light conditions. In order to minimize self shading,
20 blocks were sited along an east-west line with 3 m space between the houses and >10 m between
21 blocks, shade houses were covered with layers of 70% black shade cloth on all sides. Within shade
22 houses, seedlings were spaced 0.3 m apart. To reduce the effect of herbivory, pots were located 0.3
23 m above ground and surrounded by wire mesh to protect seedlings from mammal damage. Light
24 conditions were simulated by using either a single or triple layer of 70% black shade cloth to mimic
25 respectively (mean \pm SEM): a large gap (high; $32.9 \pm 4.5\%$ full sunlight; $127.5 \pm 13.2 \mu\text{mol m}^{-2} \text{s}^{-1}$),
26 and the forest understory (low; $2.6 \pm 0.6\%$ full sunlight; $11.7 \pm 2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) (see Saner et al.

2011 for a detailed description on the measurement of experimental light conditions). Light conditions were representative of the surrounding logged forest and slightly higher compared to previous studies as the shade cloth had worn somewhat since the shade houses were initially constructed in 2005 (Saner et al. 2011; Philipson et al. 2014; see Muff et al. 2014 for a comprehensive analysis of the difference between observed light values and the target values within replicates).

All seedlings were grown from the seeds of wild fruiting trees and propagated under nursery conditions ($\approx 11\%$ full sunlight) at the study site. To minimize intraspecific variation in initial size we chose seedlings of the same age (18 months) and a similar height of approximately 0.5 m. Seedlings were transplanted into individual pots (0.3 x 0.4 m) using topsoil that was shredded to small pieces with a rotating conveyer belt (Royer Model 110, USA) to discharge stones and woody debris. In order to prevent roots from being damaged, seedlings were kept in the original soil while transplanting. Seedlings were watered twice daily (morning and late afternoon) to avoid drought stress and fertilized twice during the course of the experiment with 2.5 g Agroblen (Scotts PBG Malaysia Sdn. Bhd., Selangor, Malaysia) 6-month slow release fertilizer (16:8:9:3, N:P:K:Mg + trace elements). They were randomly relocated every month within each shade house to avoid positioning effects. Four individuals of each of the six species in every shadehouse ($n=240$) were present at the start of the experiment in August 2006. On day 155, all seedlings in the low and high light shade houses were briefly moved into sunlit conditions. One individual per species from each shade house was then returned to the same light level, while the other was assigned to a new shade house with a different light level. This meant that half the seedlings experienced constant light conditions, either low or high for the entire experimental period, while the other half spent the first 155 days in either low or high light and the remaining 165 days in the opposite light treatment while controlling for the effect of movement between light treatments. Stem diameter (10 cm above ground) was measured at day 0, 98, 155 and 320 of the experiment (Figure 1). At day 320, all seedlings were harvested and green volume was measured to calculate wood density for each

individual plant by taking a wood sample from the lower stem following the water displacement method described in Chave (2005). Samples were then oven-dried at 60°C for one week until constant mass (note that this likely reduced total NSC levels by oven drying).

Seedling growth

Seedling growth rate analysis was done with the *nlme* package (Pinheiro and Bates 2000) in R 3.2.0 (R Development Core Team 2015). In order to estimate a seedling growth rate for each species that is unbiased by differences in initial size across species, we estimated size-specific diameter growth rates (SGR) (Nicieza and Alvarez 2009; Paine et al. 2012a). The growth rate was calculated by fitting a non-linear power law of diameter against time for each individual seedling, for details on the method see also Philipson et al. (2012, 2014). The growth rate was calculated for an average diameter (5.8 mm) across all species half-way through the experiment.

Model convergence to estimate SGR could only be achieved for seedlings grown in constant light conditions (low or high light) and which survived to the final harvest (79 individuals in total across species). Non-linear models are more difficult to fit than linear models, and in this case problems were compounded because some individuals simply did not grow in low light (Figure 1). To overcome this problem, a small number of seedlings ($n = 11$) from the low light condition were removed prior to analysis, in particular, *S. parvifolia* was removed completely.

Power laws can also be difficult to fit because of trade-offs among the three parameters: the scaling exponent (α), the growth coefficient (β), and the initial diameter (M_0). We therefore decided to restrict β to a single shared value among all species, which enabled us to fit individual growth curves to all seedlings where predictions matched the raw data for constant light environments. The selected model to estimate SGR included main effects of species ($F_{5,146} = 3.6$, $p < 0.01$) and light (treated as continuous) ($F_{1,146} = 297.2$, $p < 0.0001$). The interaction was not significant and was therefore not considered for calculating individual SGR. The best value of the growth coefficient β was 0.1, indicating that the growth was almost linear (0 = linear; 1 = exponential).

NSC and WSC analyses

Analysis of NSC concentration was only carried out on seedlings growing under two light conditions (high-light and low-light). Stem tissue from dipterocarp seedlings was shown to have slightly higher concentrations of NSC compared to the roots or leaves (O'Brien et al. 2014), and wood samples from the lower stem were used for carbohydrate analysis in the present study.

However, as the NSC extraction protocol of O'Brien et al. (2014, 2015) was different than in this study a direct comparison of the NSC and WSC concentration may not be feasible (Quentin et al. 2015). Samples were collected at the final harvest (day 320), transported to the laboratory on the day of collection and oven-dried at 60°C for one week until constant mass. Samples of >1 g dry mass were ground to fine powder in a ball mill (Tissue-Lyser, Qiagen, Germany).

Extraction of WSC

WSC were extracted twice in 1 ml of 80% and 20% ethanol (v/v), respectively, and twice in 1 ml deionized water (dH₂O) (Peters et al. 2007). For each extraction, samples were heated at 80°C for 10 min, placed on ice for 2 min, and centrifuged (15,000 g, 5 min). The supernatants of all extraction steps were pooled and adjusted to 6 ml with dH₂O. WSC (sucrose, glucose, fructose, *myo*-inositol and alditols) were then separated, identified and quantified by HPLC-PAD (Peters and Keller 2009). The remaining tissue was dried at 55°C to remove residual ethanol and subsequently used to quantify starch. Representative WSC samples were tested for lipophilic substances using a methanol-activated reverse-phase cartridge (C₁₈ Sep-Pak classic: Waters, Rapperswil, Switzerland). The HPLC chromatograms of non-delipidated and delipidated extracts were identical (data not shown), therefore we concluded that delipidation was unnecessary.

Separation and quantification of WSC

1 Aliquots (50 μ l) of WSC ethanol extracts were desalted and analyzed by HPLC-PAD (Peters &
2 Keller 2009). A Ca/Na-moderated ion partitioning carbohydrate column was used to separate WSC
3 (Benson BC-100 column; Benson Polymeric, Reno, NV, USA). It was operated at 90°C and
4 isocratically eluted with 0.005% (w/v) Ca/Na₂ – EDTA at a flow rate of 0.6 ml min⁻¹. The BC-100
5 chromatographic system consisted of a Gynkotek model 480 High Precision Pump, a Gynkotek
6 Gina 50 autosampler and a Jones column temperature controller (Ercatech, Berne, Switzerland).
7 WSC were detected after post-column addition of NaOH (300 mM, 0.6 ml min⁻¹) using an ESA
8 Coulochem II electrochemical detector (ESA, Cambridge, MA, USA), operated with an ESA 5040
9 analytical cell. WSC (sucrose, glucose, fructose, *myo*-inositol and alditols) were quantified against a
10 series of 5 nmol standard carbohydrates (Sigma Aldrich[®], Switzerland). The quantity of standard
11 carbohydrates used corresponded to the linear response range of the chromatographic system. An
12 unknown alditol (retention time: 19.1 min) was compared to a series of 5 nmol standard alditols
13 (arabitol, erythritol, threitol, xylitol, mannitol, sorbitol, dulcitol and iditol) (supplementary material
14 Figure S1). However, the latter four hexitols showed similar retention times (around 19 min), and
15 the unknown alditol was thus further analyzed by GC/MS.

17 *Derivatization of alditol*

18 For derivatization of the alditol, the desalted and lyophilized samples (20 μ l) were dissolved in a
19 mixture of 40 μ l pyridine and 10 μ l trimethylsilyl imidazole. The solution was then heated to 60°C
20 for 30 min and 1 μ l injected into a Thermo Fisher Scientific gas chromatograph-mass spectrometer
21 (GC/MS) instrument consisting of a Trace GC and a single stage quadrupole MS model DSQ. The
22 split injector was at 250°C. The GC capillary column was DB5MS (J&W Scientific, Folsom, CA,
23 U.S.A.) and was operated from 60 to 300°C at a gradient of 8°C min⁻¹. Helium was used as carrier
24 gas. The transfer line was at 250°C. Mass spectra were recorded under electron impact at 70 eV,
25 over the range 74 to 322 m/z (mass-to-charge ratio) at one scan per second for the full scan mode.
26 The chromatographic peaks were identified by injection of pure compounds. Iditol was identified

following Rivier (2003), where the relative intensity $\geq 50\%$ of the base peak has an absolute tolerance of $\pm 10\%$, and for the range between $< 50\%$ and $\geq 25\%$ the relative tolerance is $\pm 15\%$. Two fractions (217 and 319.1) with the highest m/z could only be assigned to the iditol standard for eight random samples, confirming that the alditol is indeed iditol (data not shown).

Quantification of starch

The Enzytec starch kit for food analysis was used to quantify starch (R-Biopharm, Germany). Pellets were resuspended in 5 ml double distilled water and starch was gelatinized at 110°C for 30 min. Then aliquots (20 μl) were mixed with 20 μl AGS containing α -amylglucosidase and α -amylase and incubated at 60°C for 30 min. Aliquots (120 μl) of dH_2O were added and the remaining plant debris removed by centrifugation (15,000 g, 10 min). The supernatant (120 μl) was transferred into the wells (total volume 323 μl) of a microtiter plate (Greiner clear, Huber & Co AG, Switzerland) and mixed with 80 μl of solution #1 (containing NADP^+) for the blank measurement. The enzymatic reaction was initiated with 1.5 μl of solution #2 (containing hexokinase and glucose-6-phosphate dehydrogenase). Absorbance was measured after 6 min, at 2 min intervals (reaction peak 14 min) at a wavelength of 340 nm. A glucose (Fluka[®], Switzerland) standard was used for starch quantification; starch is expressed as $\text{glucose}_{\text{eq}}$ (McCready et al. 1950). Quantification was performed on a Spectra Max M2 plate reader (Bucher Biotec, Switzerland) using the SoftMax Pro 4.7.1 (Molecular Devices, Sunnyvale, CA, USA).

Statistical analysis

In a first step, as already described above in detail, the individual seedling SGR was calculated with a linear mixed-effects model. In a second step, individual seedling SGR, wood density and NSC concentration (including starch, WSC and iditol) were then treated as dependent variables in a second linear mixed-effects model and tested against species, functional group and light treatment (fixed effects). Shade house ($n=5$) and individual shade houses ($n=10$) were treated as random

effects. Where needed, heteroscedasticity was controlled for by modelling increasing variance with the varPower function, or in the case of total NSC concentration, starch and iditol concentration the dependent variable was simply log-e transformed. In a third step, Pearson's product moment correlation was used to test for correlations between species mean values of SGR, wood density, NSC concentration and iditol concentration. NSC concentration (%), but not pool size (total mg), was included in the analyses.

Results

Growth and wood density

A significant main effect of wood density ($F_{1,35} = 121.4$, $p < 0.0001$), light condition ($F_{1,4} = 164.0$, $p = 0.0002$) and functional group ($F_{1,35} = 9.8$, $p = 0.0035$) on diameter SGR was observed, however neither two-way interactions between wood density, light condition and functional group nor the three-way interaction were found to be significant (Figure 2). The negative correlation between mean diameter SGR and mean wood density across all six species was stronger in high light ($r = 0.92$, $t = 4.6$, $df = 4$, $p = 0.01$, 95% CI: 0.99 to -0.41) compared to low light ($r = 0.85$, $t = 2.9$, $df = 3$, $p = 0.06$, 95% CI: -0.99 to 0.11) (Figure 2). Overall, an increase in light decreased wood density by 0.07 g cm^{-3} ($F_{1,4} = 11.7$, $p < 0.05$, average wood density in low-light: 0.69 g cm^{-3} , high-light: 0.62 g cm^{-3}). A light increase resulted in a marginally ($F_{1,48} = 3.6$, $p = 0.06$) higher shift in wood density in light demanders (0.13 g cm^{-3} relative change (20%): average in low light: 0.65 g cm^{-3} , average in high light: 0.52 g cm^{-3}) compared to shade tolerants (0.04 g cm^{-3} relative change (5%): average in low light: 0.73 g cm^{-3} , average in high light: 0.69 g cm^{-3}).

A positive correlation ($r = 0.96$, $t = 6.3$, $df = 3$, $p < 0.01$, 95% CI: 0.55 to 1.00) was found between species mean SGR in high-light and mean SGR in low-light conditions. Overall, the light demanders *S. argentifolia* and *S. leprosula* had a faster diameter growth rate compared to the shade-tolerants *H. nervosa* and *S. macroptera* or the generalist *D. lanceolata* (Figure 3).

1 *Relative change in NSC concentration and light acclimation*

2 Seedlings of all six species showed lower total NSC concentrations ($F_{1,4} = 60.9$, $p < 0.01$) in low-
3 light compared to the high-light condition and adjusted total NSC concentration within five months
4 of translocation (Figures 4a and d). Acclimation to a sudden light increase (gap opening) resulted in
5 a significantly different proportional increase in total NSC concentration across species ($F_{5,20} = 3.2$,
6 $p < 0.05$). Overall the shade-tolerants (including the generalist species) showed a greater relative
7 increase in NSC concentration compared to light demanders as a direct response to a simulated gap
8 opening ($F_{1,24} = 5.7$, $p < 0.05$). NSC was further separated and analysed based on components,
9 however the finding was consistent with total NSC concentrations when testing for starch
10 concentration ($F_{1,24} = 4.7$, $p < 0.05$) or WSC concentration ($F_{1,24} = 4.0$, $p = 0.06$).
11

12 *Growth and storage*

13 The relationship between the proportional increase in total NSC concentration after a gap opening
14 (Δ NSC between low and low-high condition) and the average species growth rate under the high-
15 light condition was further examined across species and functional group (Figure 5). Overall, we
16 found no significant relationship between growth and storage across species. In particular, the
17 generalist *D. lanceolata* responded with a slower growth rate and a proportionally lower relative
18 increase in total NSC concentration as a response to a gap opening. Once this species was excluded,
19 the relationship between the relative change in growth or storage was significant for the remaining
20 five species ($r = 0.96$, $t = 5.6$, $df = 3$, $p = 0.01$, 95% CI: -0.99 to -0.47). However, the light
21 demanders *S. argentifolia*, *S. leprosula* and *S. parvifolia* invested only marginally less to NSC
22 concentration compared to the shade-tolerants *H. nervosa* and *S. macropora* ($F_{1,3} = 7.6$, $p = 0.07$).
23

24 *Contribution of alditols to total NSC concentration*

25 WSC contributed 42–87% to total NSC concentration, depending on species and light condition
26 (Table 1). A main component of WSC was identified as iditol, an alditol present in all six species

and under all light conditions with a relative concentration compared to total NSC that ranged between 3-47% (mean absolute concentration: 0.1-17.8 mg g⁻¹) (Table 1). Despite the overall difference in iditol concentration between low light compared to high light conditions, the interaction between treatment and species indicated that the increase was not significant for all species ($F_{5,40} = 2.4$, $p = 0.05$) (Figure 4b and c). However, seedlings across all six species adjusted iditol concentrations within five months to their present light condition, suggesting that the trait is highly adaptive (Figure 4a and d). Seedlings that were translocated from high to low light showed a significantly lower proportional increase in iditol concentrations than seedlings that were constantly exposed to low light ($F_{1,4} = 29.5$, $p < 0.01$). Interestingly, the generalist *D. lanceolata* showed a significantly smaller increase in iditol concentration as a direct response to a gap opening compared to all other species ($F_{1,24} = 15.8$, $p < 0.0001$). Correlation between iditol concentration and other traits did not reveal any significant patterns across species and an inconsistent pattern was observed within species where a negative relationship between the relative increase in iditol concentration and wood density in the high light condition was found for three of the six dipterocarp species (*S. macroptera*, *S. argentifolia*, *S. leprosula*).

Discussion

Clearly, the selection of species and the replication within each functional group is not representative to study light niche divergence across the full ecological range with more than 250 species of dipterocarps for Borneo alone (Ashton 2004). However, based on the contrast analysis performed between functional group in response to light acclimation we can group the six dipterocarp species based on their changes in selected life history attributes into a light demanding group including *S. argentifolia*, *S. leprosula* and *S. parvifolia*; and a shade-tolerant group including *Hopea nervosa*, *S. macroptera* and the generalist *D. lanceolata*. Overall, light demanding species responded to a gap opening with increased growth and a greater relative decrease in wood density, whereas shade-tolerant species showed a greater relative increase in NSC concentration.

Investing into growth may be the single most important strategy for dipterocarps to escape the light limited environment of a tropical forest understory after a sudden gap opening (Gustafsson et al. 2016). However, in contrast to the findings of Philipson et al. (2012), who reported substantial crossovers among 21 species and no consistent growth hierarchy across light treatments, in the present study we found no crossovers in growth rates across light conditions and light demanders showed proportionally higher growth compared to shade-tolerants or the generalist species. Wright et al. (2010) and Kitajima and Bolker (2003) emphasized that seedlings that grow well in high light also show higher mortality and reduced stability and resistance in the dark. In dipterocarps, this mechanism was reported recently, where the relationship in basal diameter growth and expected probability of mortality was found to be positive, and probability of mortality also correlated negatively with wood density (Philipson et al. 2014). Testing for a growth-mortality trade-off requires a negative carbon balance or at least reduced growth in the shade as compared to light conditions (Myers and Kitajima 2007). During our experiment, none of the seedlings in the experimental treatment died and although NSC concentration was low it was not fully depleted even in low-light conditions and with little growth over ten months. For example, *S. parvifolia* seedlings did not grow in low light (Figure 3), although NSC concentration for this species was comparable to other species (Table 1 and Figure 4c). This reflects the ecology of dipterocarp seedlings, which are well known to be able to persist in the dark forest understorey close to their light compensation point for years (Watling et al. 1997; Eschenbach et al. 1998; Leakey et al. 2003). The relative change towards increased wood density across all species as a response to low-light conditions was minimal on average, but resulted in a relative change of 20% in light demanding species which could suggest that wood density may be related to avoidance of structural damage for prolonged survival, as has been proposed for bark thickness in response to fire regimes at the global scale (Pausas 2015). However, the functional role of a high wood density is yet unclear and a global assessment indicated only a weak negative relationship between wood density and

1 sapling growth (Larjavaara and Muller-Landau 2012; Philipson et al. 2014; but see Paine et al.
2 2015).

3 As dipterocarps are well known to be resistant to adverse environmental conditions the
4 proportional change in storage may support their prolonged survival under drought (O'Brien et al.
5 2014) and under light acclimation. By examining the proportional change in NSC and alditol
6 concentrations, we include additional non-structural traits that have been proposed to be related to
7 the life history strategies of tropical tree seedlings (Kobe 1997; Myers and Kitajima 2007; Poorter
8 and Kitajima 2007; Poorter et al. 2010). Our results indicate that seedlings of selected dipterocarps
9 respond to a sudden light increase with differing strategies and that the increase in NSC
10 concentration is perhaps not only a reaction to resource limitation. Whereas light demanding
11 species show a greater increase in growth to outcompete others in the race for canopy access, we
12 found that they increase proportionally less in storage. We therefore argue that the exposure to
13 sudden light changes and subsequent changes in storage levels, -such as the response to a gap
14 opening as described above, is a successful experimental approach to indicate life-history strategies
15 and associated trade-offs in key functional traits. It is important to note that the findings presented
16 here are based on a pot experiment, where seedlings in the constant high light environment showed
17 signs of being pot bound with modified roots (roots moving around the walls of the pot in a circular
18 fashion). We can therefore not conclude that the results are directly comparable to what happens in
19 the field under more natural conditions.

20 Still, little is known about the functional role of NSC and its sub-components (starch and
21 soluble sugars) in dipterocarps. The results presented here are based on lower stem tissue only and
22 do not include root or leaf NSC concentration. Dipterocarp seedlings of the species presented here
23 were shown to have slightly higher but comparable concentrations of NSC in stem compared to
24 roots or leaves (O'Brien et al. 2014, but see Quentin et al. 2015). Carbohydrate concentration in
25 dipterocarps was found to increase during drought periods and especially soluble sugars could be
26 important to avoid hydraulic failure through osmotic regulation (O'Brien et al. 2015). In our study,

1 seedlings in constant high light did not show a trade-off between growth and a proportional change
2 in NSC concentration, providing some evidence that they invest into both growth and storage when
3 light access is optimal. However, hydraulic failure is most likely to occur under adverse conditions,
4 for example during phases of water-stress or increased growth. Since the seedlings in our pot
5 experiment showed an increase in growth and proportional storage as a response to a sudden gap
6 opening we assume that: (i) NSC is continuously metabolized during the growth phase as a direct
7 response of light demanders to the light increase and therefore depleted, or (ii) the higher
8 proportional change in carbohydrates of shade-tolerants is beneficial to later stages of the seedling
9 ontogenetic development, otherwise a simultaneous relative increase in growth and storage at the
10 same time could be a more effective strategy. The first assumption may support the theory of
11 divergence in the regeneration niche, where the ecophysiology of functional group differs in the
12 response to a sudden gap opening (light niche divergence). The second assumption may support
13 ontogenetic niche shifts (Kitajima and Porter, 2008) in a constant race to gain access to the canopy
14 level.

15 Through a controlled gap opening, as can be observed in response to a sudden tree- or
16 branch-fall under natural conditions, we show that in this pot experiment light demanders tended to
17 allocate proportionally less resources into NSC, starch or WSC concentration compared to shade-
18 tolerant (including the generalist species). This led to further propose a trade-off between the
19 maximum growth rate and the proportional change in NSC concentration in response to a gap
20 opening that was supported across five out of the six species (including all light demanders and
21 shade-tolerants). A clear exception to this proposed trade-off was found in the response of *D.*
22 *lanceolata*. This species took an intermediary role by responding with a low maximum relative
23 growth rate and proportionally less NSC concentration. Interestingly, *D. lanceolata* also responded
24 to the gap opening with a significantly smaller increase in alditol concentration compared to all
25 other species. These ecophysiological responses of its proportional change in NSC and alditol
26 concentrations are the main arguments for identifying *D. lanceolata* as a generalist. The generalistic

1 response of *D. lanceolata* may not be surprising as this species is highly aromatic and young trees
2 produce a clear yellow resin known as 'oil of camphor' (Oldfield et al. 1998). We argue that the
3 investment into defense mechanisms to resist herbivory may play an important role for species that
4 do not follow the proposed trade-off in the present study (Paine et al. 2012b).

5 The functional role of alditols in dipterocarps remains unclear and further research will have
6 to address the movement of soluble sugars in response to acclimation. Würth et al. (2005) reported
7 that the relative share of mobile carbon compounds was less than 10% for carbohydrates other than
8 starch, sucrose, fructose and glucose for 17 species of adult tropical trees. Hence, it may be that the
9 observed iditol in the present study is only present at the seedling stage, where, depending on the
10 light condition, it contributed 3-47% (mean absolute concentration: 0.1-17.8 mg g⁻¹) to total NSC
11 concentration. An early study reports the occurrence of iditol in berries of mountain ash (*Sorbus*
12 *aucuparia*) which also shows ectomycorrhizal symbiosis, as is the case for dipterocarps, however
13 no indication of the physiological role was given (Plouvier 1963). In the present study, seedlings
14 that were translocated from high to low light showed proportionally lower iditol concentration
15 compared to seedlings that were constantly exposed to low light. This could suggest that iditol plays
16 a role in the adaptation of seedling metabolism in response to altered light levels, however little is
17 known about the preferential use of iditol compared to other WSCs. Iditol could also act as an
18 abiotic stress protectant when seedlings face adverse environmental conditions, for example if they
19 are exposed to a sudden gap or overshadowed by a faster growing competitor, after an insect or
20 pathogen attack (Renaud & Mauffette, 1991; Liu & Tyree, 1997), or as a result of limiting abiotic
21 conditions (Tattini *et al.*, 1996). Since dipterocarps readily form ectomycorrhizas (Saner *et al.*,
22 2010; Brearley 2012), future studies should also test for the possible role of iditol between seedlings
23 and their associated ectomycorrhiza in response to light acclimation. As alditols were shown to
24 improve stress tolerance, this may yield novel insights into mechanisms of tree species coexistence
25 at the plant physiological level in tropical forests. Although these ideas remain speculative, the
26 authors argue that the light acclimation response of iditol in *D. lanceolata* should be further

examined to test the potential role as (i) a dynamic carbohydrate buffer to support seedling growth, (ii) an abiotic stress protectant for adverse environmental conditions or (iii) an intrinsic component of the dipterocarp-ectomycorrhizal fungi symbiosis. The role of individual carbohydrate components needs be considered to understand how the diverse dipterocarp community physiologically adapts to canopy gap dynamics.

Conclusions

In conclusion, we show through a simulated gap opening in a pot experiment that selected dipterocarps can be grouped into light demanders that respond with increased growth and a greater relative decrease in wood density, whereas shade-tolerant species and a generalist show a greater relative increase in NSC concentration, including starch and WSC. Alditols were identified across all species and light levels and although their functional role remains unknown we observed that the generalist *D. lanceolata* responded to the gap opening with a smaller increase in alditol concentration compared to all other species. These findings emphasize that the understanding of the light niche divergence of these species needs to be broadened and linked to their physiology to support their effective use in large-scale forest restoration efforts.

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1 **References**

- 2 Agyeman VK, Swaine MD, Thompson J. 1999. Responses of tropical forest tree seedlings to
3 irradiance and the derivation of a light response index. *Journal of Ecology* 87:815–827.
- 4 Ashton PS. 1982. Dipterocarpaceae. *Flora Malesiana* 9:237–552.
- 5 Ashton PS. 2004. Dipterocarpaceae. In: Soepadmo E, Saw LG, Chung RCK (editors). *Tree Flora of*
6 Sabah and Sarawak. Volume 5. Sandakan, Kepong, Kuching (Malaysia): Sabah Forestry
7 Department, Forest Research Institute Malaysia and Sarawak Forestry Department.
- 8 Augspurger CK. 1984. Light requirements of neotropical tree seedlings - a comparative-study of
9 growth and survival. *Journal of Ecology* 72:777–795.
- 10 Baltzer JL, Thomas SC. 2007. Determinants of whole-plant light requirements in Bornean rain
11 forest tree saplings. *Journal of Ecology* 95:1208–1221.
- 12 Baraloto C, Forget PM. 2007. Seed size, seedling morphology, and response to deep shade and
13 damage in neotropical rain forest trees. *American Journal of Botany* 94:901–911.
- 14 Baraloto C, Goldberg DE, Bonal D. 2005. Performance trade-offs among tropical tree seedlings in
15 contrasting microhabitats. *Ecology* 86:2461–2472.
- 16 Barker MG, Press MC, Brown ND. 1997. Photosynthetic characteristics of dipterocarp seedlings in
17 three tropical rain forest light environments: a basis for niche partitioning? *Oecologia*
18 112:453–463.
- 19 Bloor JMG. 2003. Light responses of shade-tolerant tropical tree species in North-East Queensland:
20 a comparison of forest- and shadehouse-grown seedlings. *Journal of Tropical Ecology*
21 19:163–170.
- 22 Bialeski RL. 1982. Sugar alcohols. In: Loewus A. and Tanner W (editors). *Encyclopedia of plant*
23 physiology. Vol. 13a. Plant carbohydrates. I. Intracellular carbohydrates. Berlin (Germany):
24 Springer Verlag. p. 158–192.
- 25 Brearley FQ. 2012. Ectomycorrhizal associations of the Dipterocarpaceae. *Biotropica* 44:637–648.

- 1 Brokaw NVL, Scheiner SM. 1989. Species composition in gaps and structure of a tropical forest.
2 Ecology 70:538–541.
- 3 Brown N, Press M, Bebbier D. 1999. Growth and survivorship of dipterocarp seedlings: differences
4 in shade persistence create a special case of dispersal limitation. Philosophical Transactions
5 of the Royal Society B-Biological Sciences 354:1847–1855.
- 6 Brown ND, Whitmore TC. 1992. Do dipterocarp seedlings really partition tropical rain-forest gaps.
7 Philosophical Transactions of the Royal Society of London Series B-Biological Sciences
8 335:369–378.
- 9 Canham CD. 1989. Different responses to gaps among shade-tolerant tree species. Ecology 70:548–
10 550.
- 11 Canham CD, Kobe RK, Latty EF, Chazdon RL. 1999. Interspecific and intraspecific variation in
12 tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia
13 121:1–11.
- 14 Chave J. 2005. Measuring wood density for tropical forest trees; A field manual for the CTFS sites.
15 Toulouse (France).
- 16 Clearwater MJ, Susilawaty R, Effendi R, van Gardeningen PR. 1999. Rapid photosynthetic
17 acclimation of *Shorea johorensis* seedlings after logging disturbance in Central Kalimantan.
18 Oecologia 121:478–488.
- 19 Connell JH. 1978. Diversity in tropical rain forests and coral reefs - High diversity of trees and
20 corals is maintained only in a non-equilibrium state. Science, 199:1302–1310.
- 21 Dalling JW, Winter K, Hubbell SP. 2004. Variation in growth responses of neotropical pioneers to
22 simulated forest gaps. Functional Ecology 18:725–736.
- 23 Denslow JS. 1980. Patterns of plant-species diversity during succession under different disturbance
24 regimes. Oecologia 46:18–21.
- 25 Denslow JS, Ellison AM, Sanford RE. 1998. Treefall gap size effects on above- and below-ground
26 processes in a tropical wet forest. Journal of Ecology 86:597–609.

1 Dietz KJ, Keller F. 1997. Transient storage of photosynthates in leaves. In: Pessarakli M (editor).
2 Handbook of photosynthesis. New York (USA): Marcel Dekker. p. 717–737.

3 Eschenbach C, Glauner R, Kleine M, Kappen L. 1998. Photosynthesis rates of selected tree species
4 in lowland dipterocarp rainforest of Sabah, Malaysia. *Trees* 12:356–365.

5 Givnish TJ. 1988. Adaptation to sun and shade - a whole-plant perspective. *Australian Journal of*
6 *Plant Physiology* 15:63–92.

7 Gustafsson M, Gustafsson L, Alloysius D, Falck J, Sauwai Y, Karlsson A, Ilstedt U. 2016. Life
8 history traits predict the response to increased light among 33 tropical rainforest tree
9 species. *Forest Ecology and Management* 362:20–28.

10 Hartshorn GS. 1978. *Tree Falls and Tropical Forest Dynamics*. Cambridge (UK): Cambridge
11 University Press. p. 617–638.

12 Hector A, Philipson CD, Saner P, Chamagne J, Dzulkifli D, O’Brien M, Snaddon JL, Ulok P,
13 Weilenmann M, Reynolds G, et al. 2011. The Sabah Biodiversity Experiment: a long-term
14 test of the role of tree diversity in restoring tropical forest structure and functioning.
15 *Philosophical Transactions of the Royal Society B* 366:3303–3315.

16 Huante P, Rincon E. 1998. Responses to light changes in tropical deciduous woody seedlings with
17 contrasting growth rates. *Oecologia* 113:53–66.

18 Hubbell SP, Foster RB. 1992. Short-term dynamics of a neotropical forest - Why ecological
19 research matters to tropical conservation and management. *Oikos* 63:48–61.

20 Kitajima K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates
21 of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.

22 Kitajima K, Bolker BM. 2003. Testing performance rank reversals among coexisting species:
23 crossover point irradiance analysis by Sack & Grubb (2001) and alternatives. *Functional*
24 *Ecology* 17:276–281.

25 Kitajima K, Poorter L. 2008. Functional basis for resource niche partitioning by tropical trees. In:
26 Carson W, Schnitzer S (editors). *Tropical Forest Community Ecology*. Oxford (UK): Wiley-
27 Blackwell. P. 172-188.

1 Kobe RK. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling
2 survivorship and growth. *Oikos* 80:226–233.

3 Kobe RK, Pacala SW, Silander JA, Canham CD. 1995. Juvenile tree survivorship as a component
4 of shade tolerance. *Ecological Applications* 5:517–532.

5 Larjavaara M, Muller-Landau H. 2012. Still rethinking the value of high wood density. *American*
6 *Journal of Botany* 99:165–168.

7 Latham RE. 1992. Cooccurring tree species change rank in seedling performance with resources
8 varied experimentally. *Ecology* 73: 2129–2144.

9 Leakey ADB, Press MC, Scholes JD. 2003. Patterns of dynamic irradiance affect the photosynthetic
10 capacity and growth of dipterocarp tree seedlings. *Oecologia* 135:184–193.

11 Liu X, Tyree MT. 1997. Root carbohydrate reserves, mineral nutrient concentrations and biomass in
12 a healthy and a declining sugar maple (*Acer saccharum*) stand. *Tree Physiology* 17: 179–
13 185.

14 Loescher WH, Everard JD. 2000. Regulation of sugar alcohol biosynthesis. In: Leegood RC,
15 Sharkey TD and von Caemmerer S (editors). *Photosynthesis: Physiology and metabolism*.
16 Dordrecht (Netherlands): Kluwer Academic Publishers. p. 275–299.

17 Marthews TR, Burslem DFRP, Paton SR, Yangüez F, Mullins CE. 2008. Soil drying in a tropical
18 forest: Three distinct environments controlled by gap size. *Ecological Modelling* 216:369–
19 384.

20 McCready RM, Guggolz J, Silviera V, Owens MS. 1950. Determination of starch and amylose in
21 vegetables. *Analytical Chemistry* 22:1156–1158.

22 McDowell NG, Sevanto S. 2010. The mechanisms of carbon starvation: how, when, or does it even
23 occur at all? *New Phytologist* 186:264–266.

24 Moad AS. 1992. *Dipterocarp sapling growth and understorey light availability in tropical lowland*
25 *forest*. Cambridge (USA): Harvard University.

1 Muff S, Riebler A, Held L, Rue H, Saner P. 2014. Bayesian analysis of measurement error models
2 using integrated Laplace approximations. *Journal of the Royal Statistical Society Series C*
3 (Applied Statistics) 64:231–252.

4 Myers JA, Kitajima K. 2007. Carbohydrate storage enhances seedling shade and stress tolerance in
5 a neotropical forest. *Journal of Ecology* 95:383–395.

6 Newman MF, Burgess PF, Whitmore TC. 1998. *Manual of Dipterocarps for Foresters: Borneo*
7 *Island Medium and Heavy Hardwoods*. Edinburgh (UK): Royal Botanic Garden Edinburgh
8 and CIFOR.

9 Nicieza AG, Alvarez D. 2009. Statistical analysis of structural compensatory growth: how can we
10 reduce the rate of false detection? *Oecologia* 159(1):27–39.

11 O’Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014. Drought survival of tropical tree
12 seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4:710–
13 714.

14 O’Brien MJ, Burslem DFRP, Caduff A, Tay J, Hector A. 2015. Contrasting nonstructural
15 carbohydrate dynamics of tropical tree seedlings under water deficit and variability. *New*
16 *Phytologist* 205:1083–1094.

17 Oldfield S, Lusty C, MacKinnon A. 1998. *The World List of Threatened Trees*. Cambridge
18 (UK):World Conservation Press.

19 Osunkoya OO, Ash JE. 1991. Acclimation to a change in light regime in seedlings of six Australian
20 rainforest tree species. *Australian Journal of Botany* 39:591–605.

21 Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA. 2012a. How to fit
22 nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods*
23 *in Ecology and Evolution* 3:245–256.

24 Paine CET, Stenflo M, Philipson CD, Saner P, Bagchi R, Ong RC, Hector A. 2012b. Differential
25 growth responses in seedlings of ten species of Dipterocarpaceae to experimental shading
26 and defoliation, *Journal of Tropical Ecology* 28:377–384.

1 Paine CET, Amissah L, Auge H, Baraloto C, Baruffol M, Bourland N, Bruelheide H, Daïnou K, de
2 Gouvenain R, Doucet J-L, et al. 2015. Globally, functional traits are weak predictors of
3 juvenile tree growth, and we do not know why. *Journal of Ecology* 4:978–989.

4 Parsons WFJ, Knight DH, Miller SL. 1994. Root gap dynamics in lodgepole pine forest - Nitrogen
5 transformations in gaps of different size. *Ecological Applications* 4:354–362.

6 Pausas JG. 2015. Bark thickness and fire regime. *Functional Ecology* 29:315–327.

7 Peters S, Mundree SG, Thomson JA, Farrant JM, Keller F. 2007. Protection mechanisms in the
8 resurrection plant *Xerophyta viscosa* (Baker): both sucrose and raffinose family
9 oligosaccharides (RFOs) accumulate in leaves in response to water deficit. *Journal of*
10 *Experimental Botany* 58:1947–1956.

11 Peters S, Keller F. 2009. Frost tolerance in excised leaves of the common bugle (*Ajuga reptans* L.)
12 correlates positively with the concentrations of raffinose family oligosaccharides (RFOs).
13 *Plant Cell and Environment* 32:1099–1107.

14 Philipson CD, Saner P, Marthews TR, Nilus R, Reynolds G, Turnbull LA, Hector A. 2012. Light-
15 based regeneration niches: evidence from 21 dipterocarp species using size-specific RGRs.
16 *Biotropica* 44:627–636.

17 Philipson CD, Dent DH, O’Brien MJ, Chamagne J, Dzulkifli D, Nilus R, Philips S, Reynolds G,
18 Saner P, Hector A. 2014. A trait-based trade-off between growth and mortality: evidence
19 from 15 tropical trees species using size-specific relative growth rates. *Ecology & Evolution*
20 4:3675–3688.

21 Pinheiro JC, Bates DM. 2000. *Mixed-effects Models in S and S-Plus*. New York (USA): Springer
22 Verlag.

23 Plouvier V. 1963. Distribution of aliphatic polyols and cyclitols. In: Swain T (editor). *Chemical*
24 *plant taxonomy*. New York (USA): Academic Press. p. 313–336.

25 Poorter L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative
26 importance of morphological and physiological traits. *Functional Ecology* 13:396–410.

1 Poorter L. 2005. Resource capture and use by tropical forest tree seedlings and their consequences
2 for competition. In: Burslem DFRP, Pinard MA, Hartley SE (editors). Biotic Interactions in
3 the Tropics: Their Role in the Maintenance of Species Diversity. Cambridge (UK):
4 Cambridge University Press.p. 35–64.

5 Poorter L, Kitajima K. 2007. Carbohydrate storage and light requirements of tropical moist and dry
6 forest tree species. Ecology 88:1000–1011.

7 Poorter L, Kitajima K, Mercado P, Chubiña J, Melgar I, Prins HHT. 2010. Resprouting as a
8 persistence strategy of tropical trees: relations with carbohydrate storage and shade
9 tolerance. Ecology 91(9):2613–2627.

10 Quentin AG, Pinkard EA, Ryan MG, Tissue DT, Baggett LS, Adams HD, Maillard P, Marchand J,
11 Landhäusser SM, Lacointe A, et al. 2015. Non-structural carbohydrates in woody plants
12 compared among laboratories. Tree Physiology 35:1146–1165.

13 R Development Core Team. 2015. R: A Language and Environment for Statistical Computing. R
14 Foundation for Statistical Computing. Vienna (Austria): R Foundation for Statistical
15 Computing.

16 Raich JW, Christensen NL. 1989. Malaysian dipterocarp forest: tree seedling and sapling species
17 composition and small-scale disturbance patterns. National Geographic Research 5:348–
18 363.

19 Renaud JP, Mauffette Y. 1991. The relationships of crown dieback with carbohydrate content and
20 growth of sugar maple (*Acer saccharum*). Canadian Journal of Forest Research 21:1111–
21 1118.

22 Rivier L. 2003. Criteria for the identification of compounds by liquid chromatography-mass
23 spectrometry and liquid chromatography-multiple mass spectrometry in forensic toxicology
24 and doping analysis. Analytica Chimica Acta 492:69–82.

25 Sabah Forestry Departement. 2008. A Guide to Plantation Forestry in Sabah. Sandakan (Malaysia):
26 Sabah Forest Departement.

1 Sack L, Grubb PJ. 2001. Why do species of woody seedlings change rank in relative growth rate
2 between low and high irradiance? *Functional Ecology* 15:145–154.

3 Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far
4 from being resolved. *New Phytologist* 186:274–281.

5 Saner P, Philipson CD, Ong RC, Majalap N, Egli S, Hector A. 2011. Positive effects of
6 ectomycorrhizal colonization on growth of seedlings of a tropical tree across a range of
7 forest floor light conditions. *Plant Soil* 338:411–421.

8 Saner P, Loh YY, Ong RC, Hector A. 2012. Carbon stocks and fluxes in tropical lowland
9 dipterocarp rainforests in Sabah, Malaysian Borneo. *PLoS ONE*, 7(1):e29642.

10 Symington CF. 1943. *Foresters' Manual of Dipterocarps*. Kuala Lumpur (Malaysia): Penerbit
11 Universiti Malaya.

12 Tattini M, Gucci R, Romani A, Baldi A, Everard JD. 1996. Changes in non-structural carbohydrates
13 in olive (*Olea europaea*) leaves during root zone salinity stress. *Physiologia Plantarum* 98:
14 117–124.

15 Valtat A. 2015. *Tracking carbon use and allocation of non-structural carbohydrates in plant
16 response to drought*. Zürich (Switzerland): University of Zürich.

17 Watling JR, Robinson SA, Woodrow IE, Osmond CB. 1997. Responses of rainforest understorey
18 plants to excess light during sunflecks. *Australian Journal of Plant Physiology* 24:17–25.

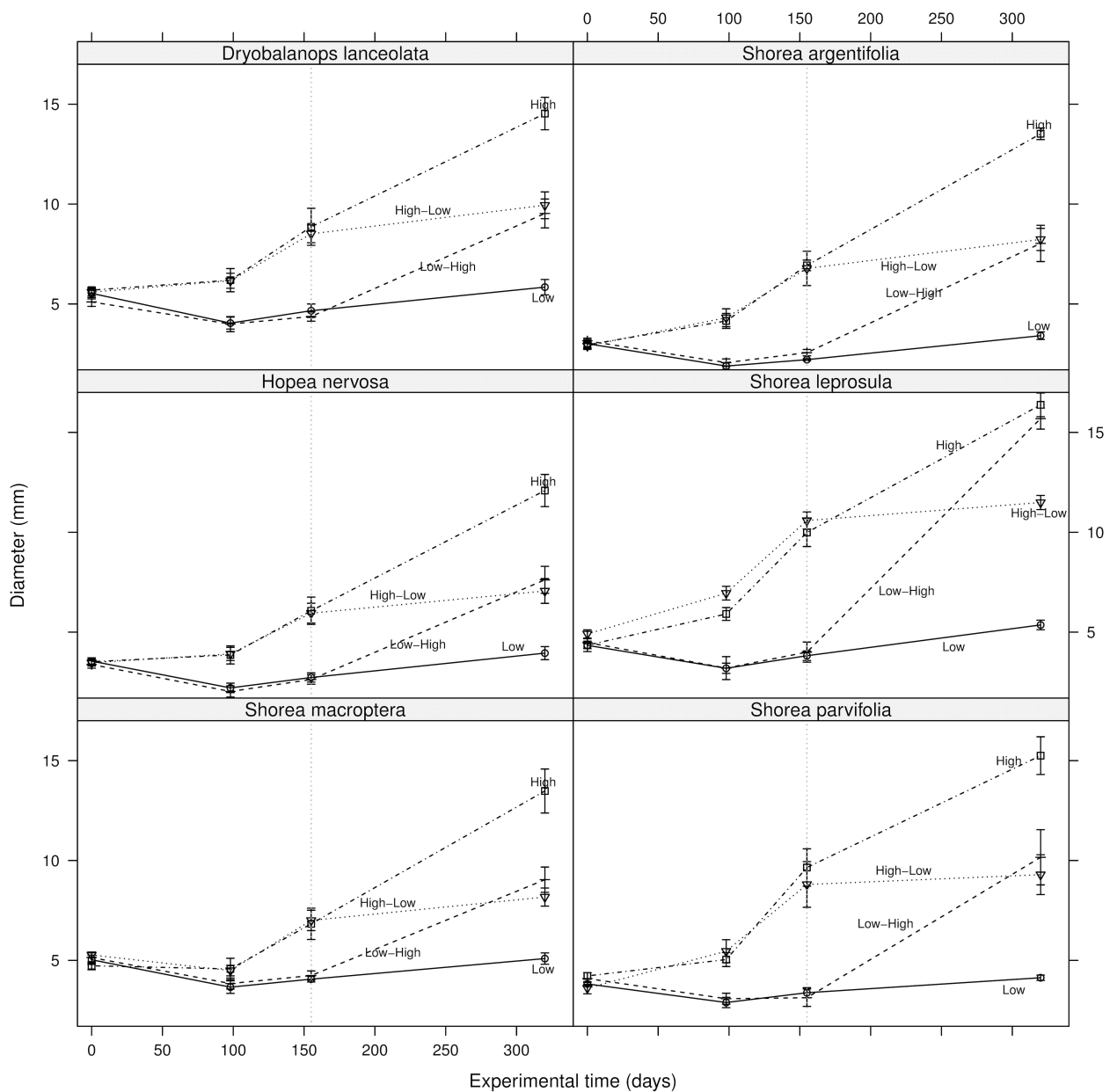
19 Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies
20 SJ, Diaz S, et al. 2010. Functional traits and the growth-mortality trade-off in tropical trees.
21 *Ecology* 91:3664–3674.

22 Würth MKR, Pelaez-Riedl S, Wright SJ, Körner C. 2005. Non-structural carbohydrate pools in
23 tropical forest. *Oecologia* 143:11–24.

24 Wyatt-Smith J. 1995. *Manual of Malayan Silviculture for Inland Forest*. 2nd ed. Kuala Lumpur
25 (Malaysia): Forest Research Institute Malaysia.

- 1 Zipperlen SW. 1997. Ecophysiology of tropical rain forest tree seedlings (Dipterocarpaceae):
- 2 growth, gas exchange and light utilisation in contrasting light environments. Sheffield (UK):
- 3 University of Sheffield.

1 **Figures**



2

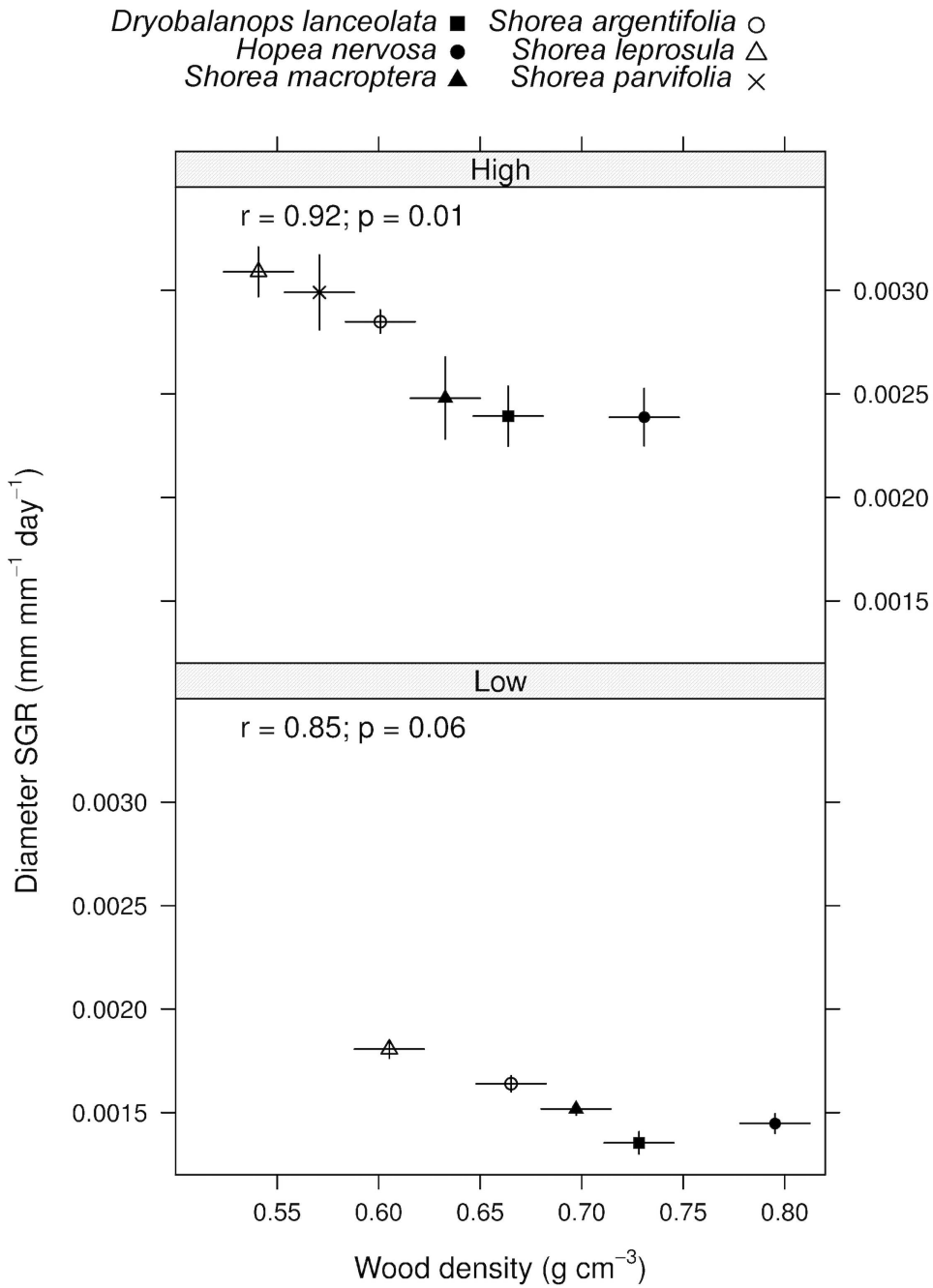
3 **Fig. 1.** Dipterocarp seedling growth over time under low- and high-light conditions grown in pots in

4 a shade-house. Seedlings of six species were non-destructively measured four times on day 0, 98,

5 155, 320. On day 155 (dotted line) seedlings were either kept under constant light condition (Low:

6 low-light, High: high-light) or switched between treatments (Low-High: low- to high-light, High-

7 Low: high- to low-light).



1

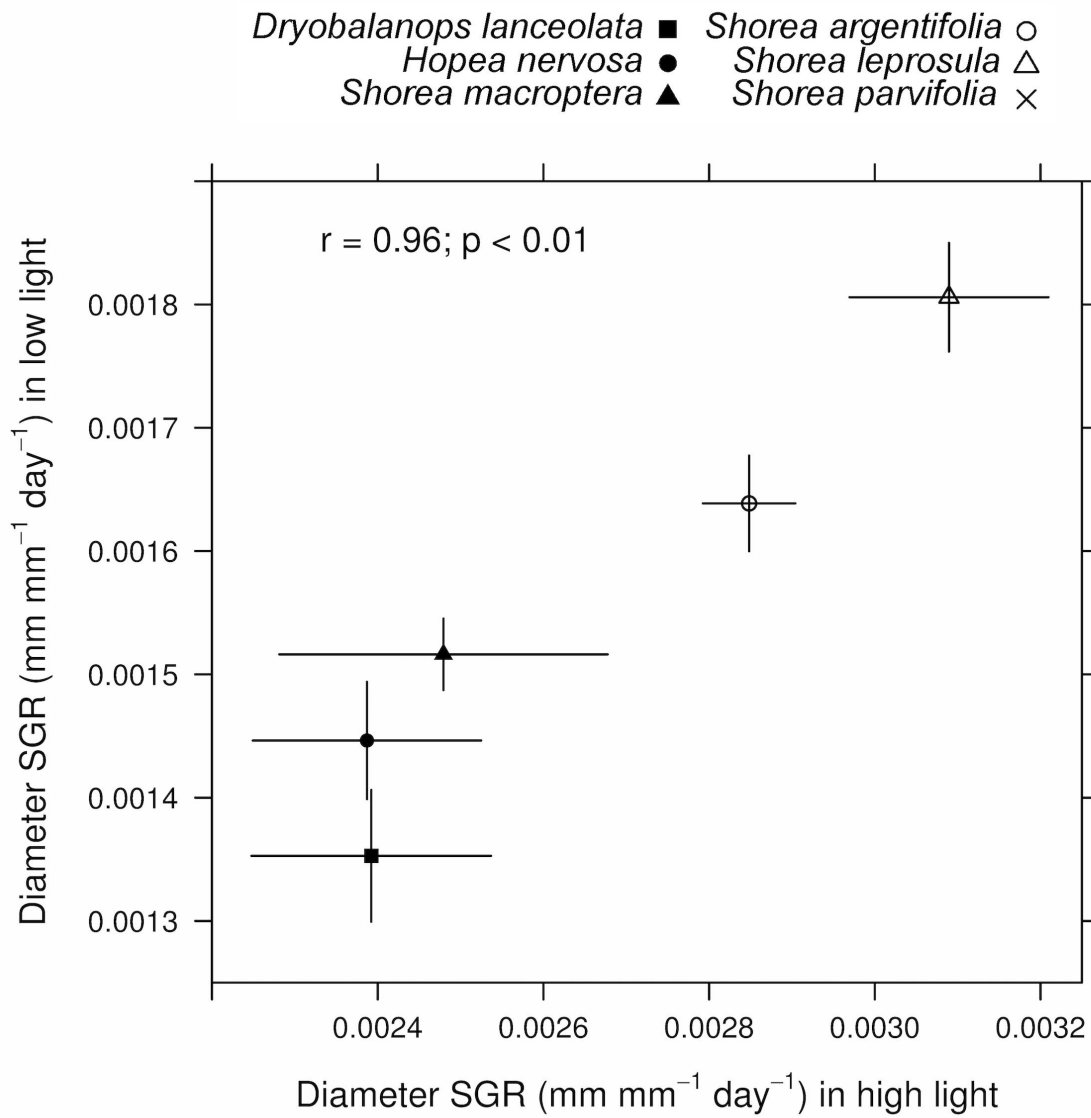
2 **Fig. 2.** Negative correlation across six dipterocarp species between mean (\pm SEM) size-specific

3 diameter growth rates (Diameter SGR) and wood density under high- and low-light condition

4 grown in pots in a shade-house. Open sympols represent the light demanders, full symbols represent

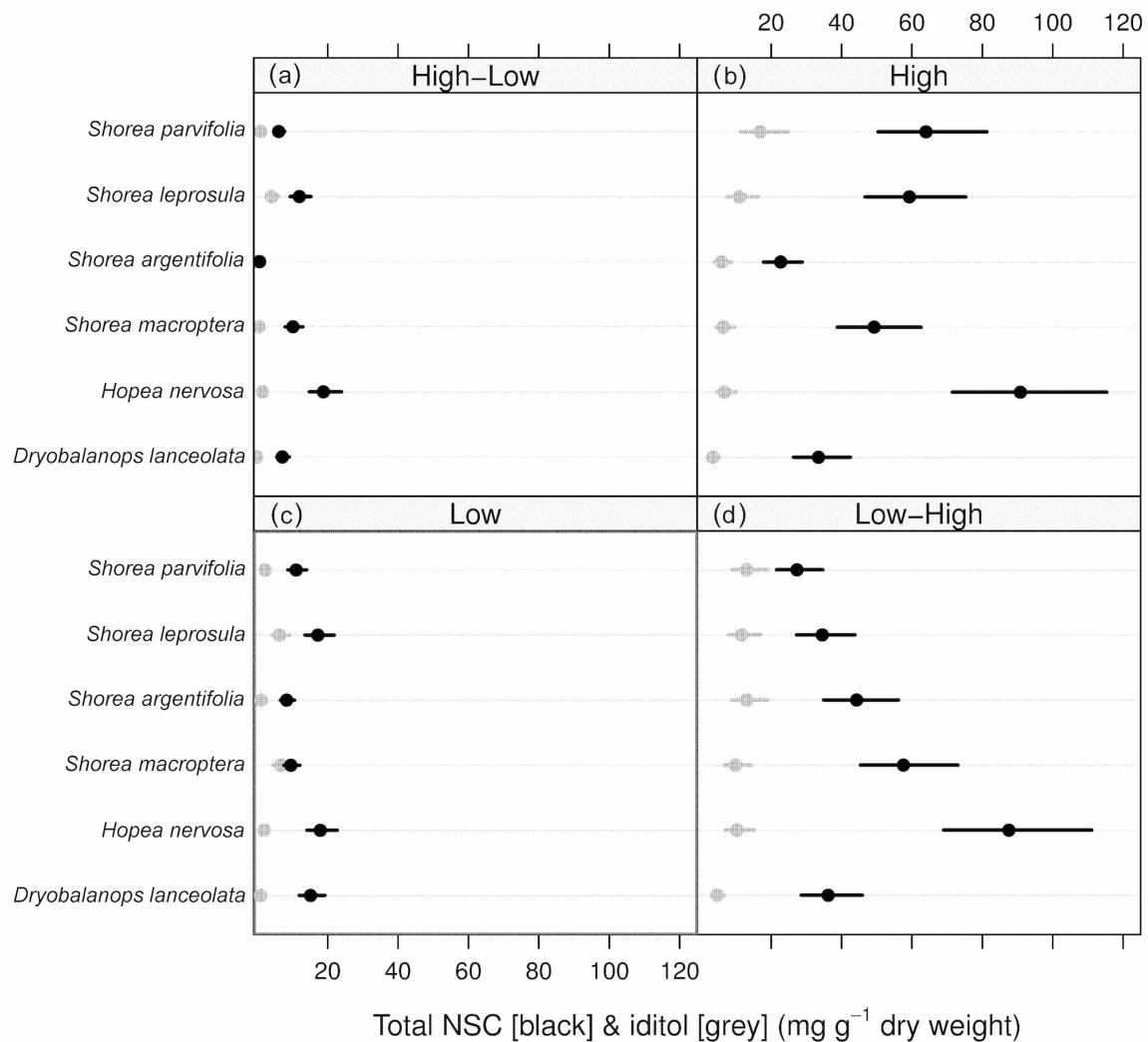
5 the shade-tolerants and the generalist. Low-light growth for *Shorea parvifolia* could not be

6 calculated and the species is therefore missing in the lower panel.

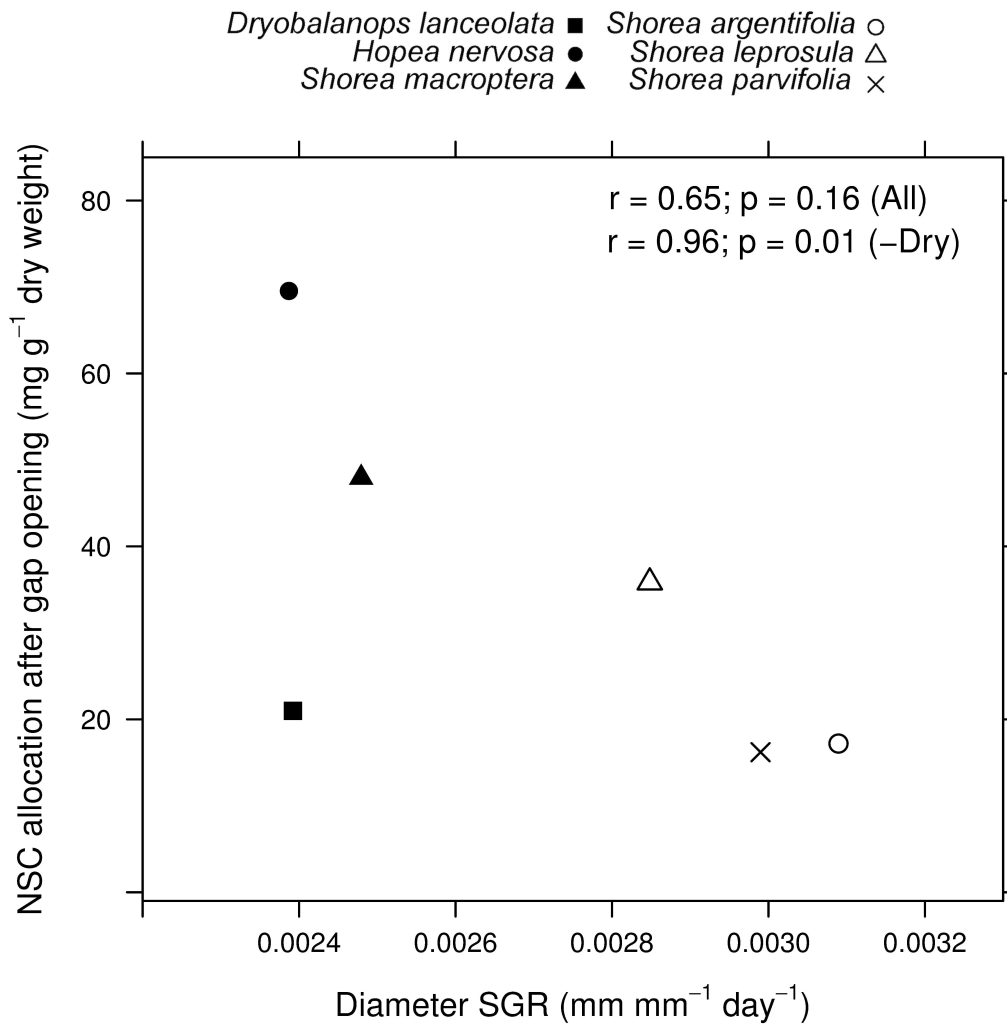


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2 **Fig. 3.** Positive correlation across six dipterocarp species between mean (\pm SEM) size-specific
 3 diameter growth rates (Diameter SGR) in contrasting light conditions (high and low) grown in pots
 4 in a shade-house. Open symbols represent the light demanders, full symbols represent the shade-
 5 tolerant and the generalist. Low-light growth for *Shorea parvifolia* could not be calculated and the
 6 species is therefore missing.



1
2 **Fig. 4.** Dimerocarp seedlings adapt NSC concentration within five months to the surrounding light
3 conditions. NSC concentration (\pm SEM; mg g⁻¹ dry weight) is reported as total NSC (black:
4 including starch and water soluble carbohydrates, WSCs) and for iditol separately (grey). Seedlings
5 were exposed to either constant high-light (b) or low-light (c) or translocated (a,d) half-way through
6 the experiment where they were grown in pots in a shade-house.



1

2 **Fig. 5.** Correlation between the proportional change in total NSC concentration (Δ NSC between
3 low and low-high condition) after a simulated gap opening and the average species growth rate
4 under high-light conditions across all six dipterocarp species grown in pots in a shade-house (All),
5 and after removing *Dryobalanops lanceolata* (-Dry).

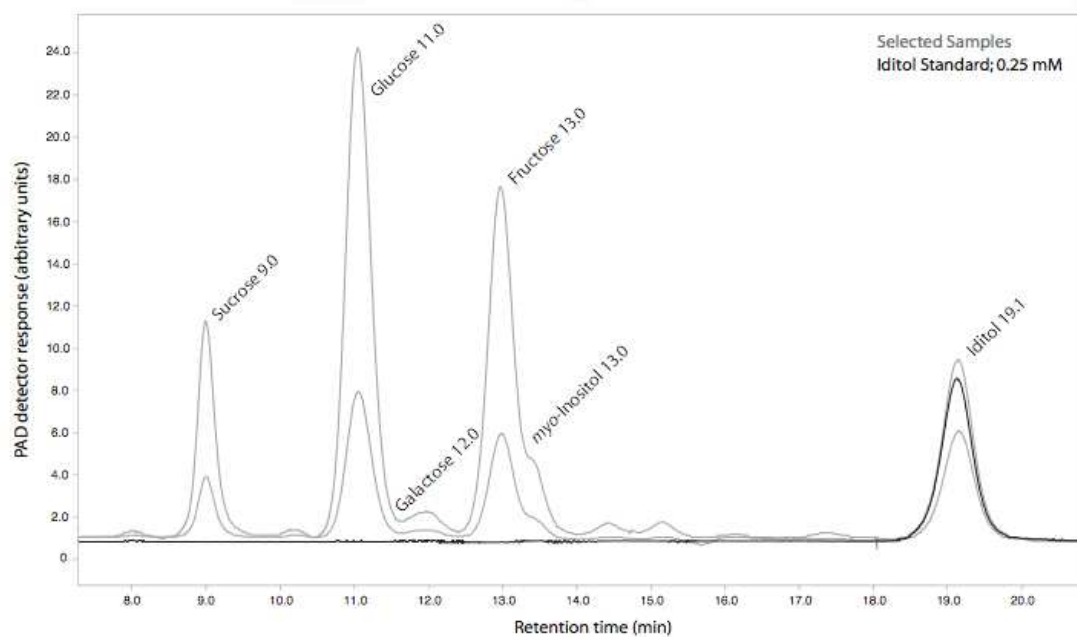


Figure S1 HPLC-PAD chromatograms of selected samples for the separation, identification and quantification of water-soluble carbohydrates (WSCs). The retention time of iditol (19.1 min) was similar to other alditols and the compound had to be further identified by GC/MS.

Tables

Table 1 Overview of total NSC concentration for all six dipterocarp species in two constant (High, Low) and two translocated (High-Low, Low-High) light conditions when grown in pots in a shade-house. Mean \pm SEM (mg g⁻¹ dry weight) are reported for starch, total water-soluble carbohydrates (WSCs), iditol and total NSC concentration. Note that iditol is included in WSCs and also reported separately for ease of interpretation. Percentage of contribution to total NSCs is shown in parentheses.

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		<i>Dryobalanops lanceolata</i>		<i>Hopea nervosa</i>		<i>Shorea macroptera</i>		<i>Shorea argentifolia</i>		<i>Shorea leprosula</i>		<i>Shorea parvifolia</i>	
Low													
	Starch	5.0 \pm 1.5	(29.9)	3.2 \pm 1.6	(15.5)	4.4 \pm 2.3	(31.2)	1.6 \pm 0.4	(18.6)	2.8 \pm 1.1	(14.8)	2.0 \pm 1.2	(13.5)
	WSC	11.7 \pm 2.6	(70.1)	17.4 \pm 3.9	(84.5)	9.7 \pm 3.1	(68.8)	7.0 \pm 1.2	(81.4)	16.2 \pm 3.6	(85.2)	12.8 \pm 5.4	(86.5)
	Iditol	1.1 \pm 0.2	(6.6)	2.1 \pm 0.5	(10.2)	0.8 \pm 0.2	(5.7)	2.2 \pm 1.3	(25.6)	8.8 \pm 3.0	(46.6)	4.7 \pm 2.8	(31.8)
	NSC	16.7 \pm 2.8	(100)	20.6 \pm 5.4	(100)	14.1 \pm 5.3	(100)	8.6 \pm 1.1	(100)	19.0 \pm 3.6	(100)	14.8 \pm 5.7	(100)
Low-High													
	Starch	14.0 \pm 3.9	(34.6)	47.5 \pm 14.8	(50.2)	13.3 \pm 3.1	(21.4)	7.0 \pm 4.4	(16.1)	18.6 \pm 1.3	(41.4)	8.0 \pm 3.2	(28.2)
	WSC	26.4 \pm 6.9	(65.4)	47.2 \pm 6.6	(49.8)	48.7 \pm 8.9	(78.6)	36.4 \pm 6.4	(83.9)	26.3 \pm 1.8	(58.6)	20.4 \pm 4.0	(71.8)
	Iditol	5.4 \pm 1.7	(13.4)	12.0 \pm 2.6	(12.7)	10.8 \pm 2.5	(17.4)	12.5 \pm 2.4	(28.8)	13.7 \pm 1.4	(30.5)	12.9 \pm 1.7	(45.4)
	NSC	40.4 \pm 10.6	(100)	94.7 \pm 17.5	(100)	62.0 \pm 11.4	(100)	43.4 \pm 9.3	(100)	44.9 \pm 1.2	(100)	28.4 \pm 7.2	(100)
High-Low													
	Starch	5.0 \pm 1.7	(56.2)	3.8 \pm 1.4	(19.2)	2.7 \pm 0.9	(24.1)	0.6 \pm 0.2	(54.5)	5.1 \pm 0.7	(40.5)	2.5 \pm 1.1	(34.7)
	WSC	3.9 \pm 1.2	(43.8)	16.0 \pm 1.9	(80.8)	8.5 \pm 2.0	(75.9)	0.5 \pm 0.1	(45.5)	7.5 \pm 1.4	(59.5)	4.7 \pm 0.8	(65.3)
	Iditol	0.3 \pm 0.1	(3.4)	1.9 \pm 0.3	(9.6)	1.0 \pm 0.3	(9)	0.1 \pm 0.01	(9.1)	4.6 \pm 0.8	(36.5)	1.6 \pm 0.5	(22.2)
	NSC	8.9 \pm 2.2	(100)	19.8 \pm 2.8	(100)	11.2 \pm 1.8	(100)	1.1 \pm 0.3	(100)	12.6 \pm 1.4	(100)	7.2 \pm 1.7	(100)
High													
	Starch	16.5 \pm 3.6	(48.8)	50.0 \pm 15.2	(51.1)	15.1 \pm 2.5	(29.7)	8.4 \pm 3.7	(35.4)	35.0 \pm 9.3	(57.8)	31.7 \pm 7.6	(46.3)
	WSC	17.3 \pm 2.1	(51.2)	47.9 \pm 9.2	(48.9)	35.8 \pm 6.3	(70.3)	15.3 \pm 1.0	(64.6)	25.5 \pm 5.4	(42.2)	36.8 \pm 6.2	(53.7)
	Iditol	3.7 \pm 0.1	(10.9)	7.7 \pm 1.9	(7.9)	6.9 \pm 0.9	(13.6)	6.2 \pm 0.3	(26.2)	12.1 \pm 2.4	(20)	17.8 \pm 2.9	(26)
	NSC	33.8 \pm 1.7	(100)	97.9 \pm 18.3	(100)	50.9 \pm 6.1	(100)	23.7 \pm 3.3	(100)	60.5 \pm 5.8	(100)	68.5 \pm 11.5	(100)

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